



Trade-off of energy metabolites as well as body color phenotypes for starvation and desiccation resistance in montane populations of *Drosophila melanogaster*

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ABSTRACT

Storage of energy metabolites has been investigated in different sets of laboratory selected desiccation or starvation resistant lines but few studies have examined such changes in wild-caught populations of *Drosophila melanogaster*. In contrast to parallel selection of desiccation and starvation tolerance under laboratory selection experiments, opposite clines were observed in wild populations of *D. melanogaster*. If resistance to desiccation and starvation occurs in opposite directions under field conditions, we may expect a trade-off for energy metabolites but such correlated changes are largely unknown. We tested whether there is a trade-off for storage as well as actual utilization of carbohydrates (trehalose and glycogen), lipids and proteins in *D. melanogaster* populations collected from different altitudes (512–2500 m). For desiccation resistance, darker flies (>50% body melanization) store more body water content and endure greater loss of water (higher dehydration tolerance) as compared to lighter flies (<30% body melanization). Based on within population analysis, we found evidence for coadapted phenotypes i.e. darker flies store and actually utilize more carbohydrates to confer greater desiccation resistance. In contrast, higher starvation resistance in lighter flies is associated with storage and actual utilization of greater lipid amount. However, darker and lighter flies did not vary in the rate of utilization of carbohydrates under desiccation stress; and of lipids under starvation stress. Thus, we did not find support for the hypothesis that a lower rate of utilization of energy metabolites may contribute to greater stress resistance. Further, for increased desiccation resistance of darker flies, about two-third of total energy budget is provided by carbohydrates. By contrast, lighter flies derive about 66% of total energy content from lipids which sustain higher starvation tolerance. Our results support evolutionary trade-off for storage as well as utilization of energy metabolites for desiccation versus starvation resistance in *D. melanogaster*.

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1. Introduction

In various drosophilid flies, clinal patterns result due to action of natural selection on different quantitative traits (Endler, 1986; Mousseau et al., 2000). Repeatability of clines on different continents provides further evidence that genetic differences between populations are primarily caused by natural selection and not due to genetic drift (Hoffmann and Weeks, 2007). On the Indian subcontinent, various *Drosophila* species show opposite clines for desiccation and starvation resistance (Parkash and Munjal, 1999, 2000) but there is lack of repeatability of such clines on other continents such as Australia and South America (Robinson et al., 2000; Hoffmann et al., 2001; Hoffmann and Weeks, 2007). Further, for desiccation and starvation resistance, selection responses differ under field versus laboratory selection. For example, laboratory selection experiments have shown parallel selection of starvation and desiccation resistance in *Drosophila melanogaster*

(Chippindale et al., 1996, 1998; Hoffmann and Harshman, 1999). Under laboratory conditions, storage and use of common energy metabolites might have induced parallel changes for starvation and desiccation resistance. In contrast, causal factors and storage of energy metabolites might be different under wild conditions which could be responsible for opposite clines. Thus, it is not clear whether desiccation and starvation resistance are the target of selection or result due to correlated response of natural selection acting on other physiological traits in *D. melanogaster*.

In ectothermic organisms, survival under desiccation or starvation stress can be maximized due to acquisition of resources such as water and/or energy metabolites (Gibbs et al., 1997; Chippindale et al., 1998; Djawdan et al., 1998; Klowden, 2007). Laboratory selected desiccation resistant strains of *D. melanogaster* store metabolites which provide metabolic water to compensate water loss (Gibbs et al., 1997, 2003). In contrast, lipids accumulate during starvation selection (Chippindale et al., 1996; Rion and Kawecki, 2007; Arrese and Soulages, 2010) and provide two times more energy per gram than carbohydrates (Withers, 1992). However, in diverse insect taxa, data on accumulation of energy metabolites for desiccation or

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starvation resistance always do not match such expectations. For example, large sized insects (locusts and tse-tse flies) as well as small sized mosquitoes store and use lipids under dehydration stress (Loveridge and Bursell, 1975; Nicolson, 1980; Benoit et al., 2010). Desiccation selection experiments have reported different storage patterns of energy metabolites in *D. melanogaster* (Hoffmann and Parsons, 1993; Telonis-Scott et al., 2006). For example, some studies have evidenced increased level of glycogen reserves in selected lines as compared with control (Chippindale et al., 1998; Djawdan et al., 1998; Folk et al., 2001). However, in another study, desiccation selected strains showed higher lipid content but there was no difference for glycogen content in selected versus control lines (Telonis-Scott et al., 2006). Therefore, there is lack of consensus for storage of energy metabolites in laboratory selected desiccation resistant strains of *D. melanogaster*. Further, association between lipid content and starvation resistance has also shown inconsistent patterns (Hoffmann et al., 2001; Rion and Kawecki, 2007). Laboratory selection of higher starvation resistance in *D. melanogaster* has evidenced an increase in lipid storage (Chippindale et al., 1996; Harshman et al., 1999). In contrast, *Drosophila* larvae raised under crowding conditions showed higher lipid content without improving starvation tolerance (Baldal et al., 2005). Similarly, there is lack of correlation between lipid content and starvation resistance in wild populations of *D. melanogaster* from Australia (Hoffmann et al., 2001). Thus, it is not clear whether desiccation and starvation resistance are associated with storage of similar or different energy metabolites.

Several studies on desiccation selected laboratory strains of *D. melanogaster* have shown significant increase in glycogen content in the adult flies (Graves et al., 1992; Gibbs et al., 1997; Chippindale et al., 1998; Djawdan et al., 1998; Hoffmann and Harshman, 1999). In *D. melanogaster*, higher desiccation resistance of D strains results due to accumulation of more carbohydrate contents during the pre-adult (larval) stage (Gefen et al., 2006). The role of increased glycogen store in desiccation resistant strains has been explained on the basis of bound water hypothesis (Gibbs et al., 1997; Folk et al., 2001; Gibbs, 2002; Folk and Bradley, 2005). According to Gibbs and co-workers, (D) strains contain about ~50% of total water content in bound water form (Gibbs et al., 1997). Thus, under desiccation stress, metabolism of glycogen can release water of hydration for maintenance of water balance. However, these studies did not consider intracellular location of glycogen and its possible effects on water balance in *D. melanogaster*. Folk and coworkers showed that desiccation resistance of D strains is significantly correlated with hemolymph volume as well as carbohydrate contents (Folk et al., 2001). Further, higher carbohydrates in D flies showed significant correlation with extracellular hemolymph volume but not with intracellular water volume. Since, glycogen is stored within cells and 80% of insect trehalose occurs in hemolymph, it was suggested that increase in carbohydrates content in D flies might reflect increase in trehalose content (Folk et al., 2001). To the best of our knowledge, changes in the trehalose level have not been examined in control versus desiccation selected strains and also in wild populations of *D. melanogaster*.

Utilization of stored energy metabolites under stressful conditions has fitness consequences in laboratory selected strains (Hoffmann and Harshman, 1999; Harshman and Hoffmann, 2000; Gibbs and Gefen, 2009) but this aspect has received lesser attention for wild populations of *Drosophila* species (Gibbs, 2002). A single study has investigated utilization of energy metabolites (carbohydrates, lipids and proteins) as a function of different durations of desiccation or starvation stress for three mesic and two desert *Drosophila* species (Marron et al., 2003). This study showed utilization of both lipids and proteins under starvation or desiccation stress but there was seven-fold higher utilization of carbohydrates under desiccation as compared to starvation stress. Further, based on the results of ANCOVA (body mass as a covariate), stored levels of carbohydrate

or lipid contents did not vary between cactophilic and mesic *Drosophila* species (Marron et al., 2003). In contrast, utilization of energy metabolites in geographical populations of *D. melanogaster* is largely unknown.

For clinal variation in quantitative traits, it is not clear whether natural selection selects each trait independently or several related traits coevolve to maximize fitness under wild conditions (Angilletta, 2009). In *Drosophila*, tropical versus temperate habitats select contrasting patterns for several traits such as body size, body color and tolerance to cold versus heat stress (Chown and Nicolson, 2004). However, it is not clear whether such diverse traits coevolve or not. In ectothermic organisms, coevolution of morphological and physiological traits has formed the basis of coadaptation hypothesis (Angilletta, 2009). Coadapted traits are represented by associations between body melanization and thermo-resistance in *D. melanogaster* (Parkash et al., 2010). Further, possible associations between body melanization and other stress related traits are not known. If eco-physiological traits and body melanization coevolve, we may expect within-population associations between body color phenotypes and stress-related traits in *D. melanogaster*. Thus, we tested the hypothesis whether there are coadapted evolutionary changes in body color phenotypes and energy metabolites for conferring resistance to starvation or desiccation stress.

For analysis of stress resistance traits, several studies have focused on latitudinal gradients while altitudinal transects have received lesser attention (Sørensen et al., 2005; Collinge et al., 2006). There are rapid changes in climatic conditions over a relatively small distance along altitude; and between populations differences in stress related traits have been attributed to natural selection (Parkash et al., 2005). In the present work, we analyzed various ecophysiological traits (body melanization; measures of water balance; and storage as well as utilization of energy metabolites under starvation and desiccation stress) in montane populations of *D. melanogaster*. For testing associations between melanization and desiccation resistance, measures of water balance were investigated in darker and lighter isofemale lines of *D. melanogaster*. Based on within population analysis, correlations were examined between darker as well as lighter phenotypes with stress resistance traits and energy metabolites. Further, flies were tested for simultaneous or alternate use of energy metabolites when exposed to different durations of desiccation or starvation stress. We examined whether there is trade-off of total energy budget in terms of carbohydrates and lipids in darker versus lighter flies. Thus, the present work assessed whether *D. melanogaster* populations collected from different altitudes show independent or coadapted changes in body color phenotypes, stress-related traits and energy metabolites.

2. Materials and methods

2.1. Collections and cultures

Wild individuals of *D. melanogaster* (n = 350–400 flies from each site) were collected in September, 2009 by net-sweeping method in a single trip from six montane localities (latitudinal range: 29°47'–32°33' N; longitudinal range: 76°57'–77°21' E; altitudinal range: 512–2500 m) of the western Himalayas (Table 1). Wild-caught females were used to initiate isofemale lines (20 lines per population). All cultures were maintained at low density (60–70 eggs per vial of 40 × 100 mm size) on cornmeal-yeast-agar medium at 21 °C. All experiments were performed with G₆ and G₇ generations on eight days old virgin female flies. Climatic data for thermal variables of origin of populations were obtained from Indian Institute of Tropical Meteorology (IITM; www.tropmet.res.in) but data on relative humidity were obtained from 'Climatological Tables' published by the Indian Meteorological Department, Govt. of India, New Delhi.

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